

Climate-induced changes in the stem form of 5 North American tree species

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ABSTRACT

Generally, the effects of climate change on tree growth focus on changes in one dimension of a tree. However, diameter increment along the main stem reacts differently to climatic variables, which in turn influences tree form. These differences can thus have important implications on stem volume, which could induce biases in future forest biomass estimation. A stem taper model including climatic variables was fitted to stem analysis data of five different species (*Abies balsamea*, *Betula papyrifera*, *Picea glauca*, *Picea mariana*, *Populus tremuloides*) distributed along a gradient from the temperate to the boreal forest of Eastern Canada. The effects of shifts in stem form on tree volume between different climatic scenarios were then estimated and related to different functional traits. Changes in stem form with climatic variables were observed for four of the five species, with up to 5% differences in stem volume between different climatic situations. Changes in stem volume were found to decrease with increasing waterlogging and shade tolerance. The most important differences in stem volume can induce changes of 3–4% in the biomass of a single tree. Not taking into account shifts in stem form could have implications in forest biomass estimations.

1. Introduction

According to the optimal partitioning theory (Thornley, 1972; McCarthy and Enquist, 2007), plants, and especially woody species, preferentially allocate their growth to the compartment (i.e. stem, branches, foliage, roots) which acquires the resource that is the most limiting to their growth. For example, a plant that is in a shaded environment will preferentially allocate its resources to increase its capacity in intercepting light, whereas plants in poor soils will expand their underground exploration (through root development or mycorrhizae). Moreover, plants change their allocation patterns with both environmental and local factors such as trees that reduce their foliage area in order to decrease their vulnerability to cavitation in arid conditions (Maherali and DeLucia, 2001) or increase their allocation to the roots in order to improve nutrient uptake in cold climates (Reich et al., 2014).

Moreover, the growth distribution within a given compartment also varies, which in turn can have important implications for estimating plant biomass. For example, foliage area is intimately related to the sapwood cross sectional area of the main stem (Shinozaki et al.,

1964b,a). Thus changes in foliage distributions help to understand shifts in tree stem form (Schneider et al., 2011a). The changes in the biomass allocation along the stem can also be explored through the study of the vertical growth profiles of a tree stem (Goudiaby et al., 2012). A few studies have worked on establishing such growth distributions within a tree stem at an annual level (Deleuze and Houllier, 2002; Cortini et al., 2013). When not considering butt flare, the growth rate is generally the largest at the crown base, in accordance with Pressler's law (Larson, 1963).

The within-compartment foliage distribution is known to be under the control of a large panel of factors, among them tree species, tree size, site conditions and competition (Schneider et al., 2011b). As for the main tree stem, both height and diameter growth have been shown to be closely related to temperature (Andalo et al., 2005; Goldblum and Rigg, 2005; Huang et al., 2010; Messaoud and Chen, 2011; O'Neill and Nigh, 2011; Girard et al., 2014) while the influence of precipitation was not as clear, at least in northern climates (Franceschini et al., 2016).

Instead of considering the longitudinal stem growth distributions, foresters generally use stem taper, defined as the diameter along the stem which corresponds to the cumulative sum of the annual growth at

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a given height. It has long been known that trees have more taper in open or in more fertile forests (Larson, 1963). Recent studies have shown that stem form is also influenced by climatic conditions (Nigh and Smith, 2012).

Shifts in stem form is often associated to changes in tree crown structure, as it has been demonstrated through modelling approaches (Valentine et al., 2012). The importance of crown characteristics have been explained by both hormonal (e.g. Larson, 1963) and biomechanical theories (e.g. Fournier et al., 2013). The first theory relies on the importance of auxins in general, and indole-3-acetic acid (IAA) in particular, on the initiation of radial growth of the stem (Nilsson et al., 2008). As IAA is formed in the apical meristems (Zhao, 2010), the xylem close to the apical meristems will receive the signal to initiate secondary growth earlier and thus have longer growth periods, thus leading to larger increments of the stem at crown base. The biomechanical theory on the other hand assumes that the stem must support both the branches and foliage to avoid buckling (Niklas, 2013). As a consequence, trees with bigger crowns must have larger diameter stems, and hence a larger stem increment at the base of the crown is required.

Changes in tree form have implications in estimating above ground biomass, as the main stem of the tree can account for up to 70% of a tree's biomass (Poorter et al., 2012). In order to estimate the above-ground biomass of a given tree, the volume of each compartment is generally multiplied by its basic density. Most studies have until recently focused on solely the changes in wood density with climatic variables (Franceschini et al., 2013), with very little attention on changes in tree forms. There are indications that the response of tree species to changes in climatic variables are determined by certain functional traits (Franceschini et al., 2016). Thus if tree form shifts with global changes, it should also be important to consider the effect of climate as forecasted by the International Panel on Climate Change (IPCC) on stem taper and volume. It is thus important to evaluate the magnitude of the climatic dependency of volume in order to avoid biases in the estimation of future biomass.

The present study has the objective to estimate the effects of climatic variables on tree volume for the main commercial species growing in northeastern America. This was performed by (i) integrating climatic variables in a previously published stem taper equation (Schneider et al., 2013); (ii) converting stem taper into volume (Fortin et al., 2013); (iii) compare the effects of different global change scenarios on tree volume and biomass estimates. The tested hypothesis is that stem taper decreases with temperature and increases with precipitations. We also hypothesized that global change will result in increases in tree volume and tree biomass for a given dbh and tree height which will be higher for conifers than for broadleaves. The analysis however relies on the assumption that the influence of future climatic conditions on tree development will remain constant.

2. Materials and methods

2.1. Study area

The database used in this study was originally collected to establish links between site fertility and forest ecotypes (Laflièche et al., 2013). A total of 8558 trees in 1328 plots distributed over a land base of 761,000 km² in the province of Quebec, Canada, were used to fit stem taper models (Table 1). The studied species were white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* Moench. Voss), black spruce (*Picea mariana* Mill. Britton), trembling aspen (*Populus tremuloides* Michx.) and balsam fir (*Abies balsamea* L. Mill). The study area ranges (Fig. 1) from the sugar maple-basswood bioclimatic domain in the temperate forests to the south to the black spruce-moss domain in boreal forest to the north (e.g. between 45° and 51°N) and between the eastern and western borders of the province of Quebec, Canada (i.e. 60° and 80°W).

Table 1

Dataset statistics (standard deviations in parentheses) and species functional traits (Waterlogging and drought tolerance: Niinemets and Valladares (2006); Shade tolerance: Humbert et al. (2007)).

	Trembling aspen	White birch	White spruce	Black spruce	Balsam fir
Number of plots	258	134	312	562	645
Number of trees	799	657	1321	2802	2979
Mean diameter at breast height (mm)	288 (60)	197 (48)	289 (68)	193 (43)	221 (47)
Mean total tree height (m)	22.41 (2.84)	17.44 (2.44)	18.86 (3.57)	15.71 (2.84)	16.74 (2.90)
Mean altitude (m)	336 (99)	373 (104)	428 (188)	420 (127)	421 (181)
Mean annual precipitation sum (mm)	1010 (93)	1023 (98)	1072 (123)	982 (77)	1059 (112)
Mean annual temperature (°C)	1.91 (1.22)	1.75 (1.19)	1.64 (1.32)	0.22 (1.12)	1.31 (1.55)
Waterlogging tolerance	2	1.25	1.02	2	1.77
Drought tolerance	1	2.02	2.88	2	1.77
Shade tolerance	9	7	4	4	3

2.2. Data collection

A stratified random sampling design was used to select the sample trees. The five most important ecotypes were identified in each ecological region of the province based on the forest ecological classification system established by the Quebec Ministry of Natural Resources (Robitaille et al., 2015). Within these ecotypes, a minimum of 5 temporary sample plots of 400 m² were established. A forest inventory within these plots was carried out where the species and diameter at breast height (DBH) of all the living trees were recorded in order to obtain stand basal area (BA, m².ha⁻¹) and density (SD, stems.ha⁻¹).

Sample trees were then randomly selected within a 25-m radius from the plot centre, whereby the trees had to belong to the dominant species of the ecotype, be a dominant or codominant tree, not have any forks nor decay and a relatively straight main stem. On average, between five and ten trees per plot were chosen. The DBH (mm) of the sample trees was measured. Once the tree felled, total height (HT, m) was taken and disks cut out at 0.15, 0.60, 1.00, 1.30, 3.00 m and every 2 m until the stem apex. The disk diameter was measured with a circumference tape, as well as bark width at four points in order to obtain the under bark diameter of the cross section (d, mm).

2.3. Stem taper model

The stem taper model used is based on the work of Schneider et al. (2013). It is an adaptation of the model originally proposed in Sharma and Oderwald (2001) and later modified by Sharma and Zhang (2004). The model relates the under bark diameter d (in mm) at any point along the stem to DBH (in mm), HT (in m) and the height at which diameter d is taken (h, m) as follows

$$d_{ijk}^2 = \frac{1}{1 + e^{(\alpha + b_{i,1} + b_{ij,1})}} \times DBH_{ij}^2 \times \left(\frac{HT_{ij} - h_{ijk}}{HT_{ij} - 1.3} \right) \times \left(\frac{h_{ijk}}{1.3} \right)^{2 - (x_{ijk}\beta + b_{i,2} + b_{ij,2})} + \varepsilon_{ijk} \quad (1)$$

for $i = 1, 2, \dots, q$; $j = 1, 2, \dots, n_i$ and $k = 1, 2, \dots, o_{ij}$.

Where:

- α and β are a fixed effect or a vector of fixed effects parameters estimated by the regression, respectively,
- q , n and o_{ij} the total number of plots, the total number of trees and the number of disks in the tree i of plot j , respectively.
- i , j , and k the plot, tree within plot and disk within tree within plot indices, respectively, such that

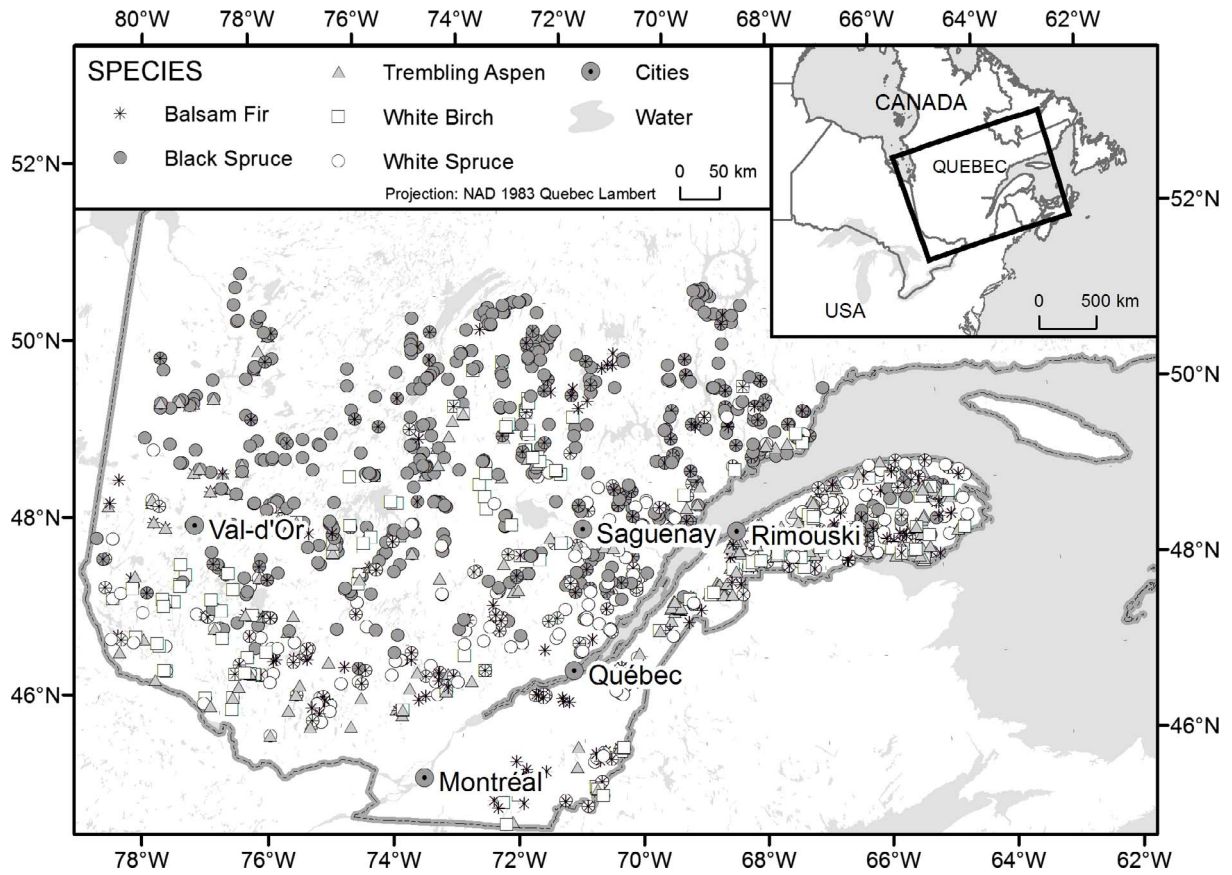


Fig. 1. Locations of the sample plots for each species.

– $b_{i,1}$ and $b_{i,2}$ plot random effects where:

$$\mathbf{b}_i = (b_{i,1}, b_{i,2})^T \sim N_2(\mathbf{0}, \mathbf{G}_{\text{plot}})$$

$$\mathbf{G}_{\text{plot}} = \begin{bmatrix} \sigma_{\text{plot},1}^2 & \rho_{\text{plot}} \sigma_{\text{plot},1} \sigma_{\text{plot},2} \\ \rho_{\text{plot}} \sigma_{\text{plot},1} \sigma_{\text{plot},2} & \sigma_{\text{plot},2}^2 \end{bmatrix}$$

– $b_{ij,1}$ and $b_{ij,2}$ tree random effects where:

$$\mathbf{b}_{ij} = (b_{ij,1}, b_{ij,2})^T \sim N_2(\mathbf{0}, \mathbf{G}_{\text{tree}})$$

$$\mathbf{G}_{\text{tree}} = \begin{bmatrix} \sigma_{\text{tree},1}^2 & \rho_{\text{tree}} \sigma_{\text{tree},1} \sigma_{\text{tree},2} \\ \rho_{\text{tree}} \sigma_{\text{tree},1} \sigma_{\text{tree},2} & \sigma_{\text{tree},2}^2 \end{bmatrix}$$

– ε_{ijk} the residual error, where

$$\varepsilon_{ij} = (\varepsilon_{ij1}, \varepsilon_{ij2}, \dots, \varepsilon_{ijk})^T \sim N_k(\mathbf{0}, \Psi_{ij}^{1/2} \Lambda_{ij} \Psi_{ij}^{1/2})$$

which depends on a correlation (Ψ) and variance (Λ) matrix. The complete description of the model is given in [Appendix 1](#).

2.3.1. Fixed effects

The fixed effects of the model are α and β , the latter being decomposed into position-, tree- and plot-level terms:

$$\mathbf{x}_{ijk} \beta = \beta_0 + \mathbf{x}_{ijk}^{\text{position}} \beta^{\text{position}} + \mathbf{x}_{ij}^{\text{tree}} \beta^{\text{tree}} + \mathbf{x}_i^{\text{plot}} \beta^{\text{plot}} \quad (2)$$

Position variables include some type of relative position within the tree, tree level variables include DBH and HT whereas the plot level variables include stand basal area, stand density, and ecological classification variables. Each term is described in detail in [Appendix 1](#).

2.4. Climatic effects on stem taper

Climatic variables could be introduced into the model either through the fixed parameters α or β_0 . Both options were investigated by expressing these two parameters as linear combination of climatic variables, considering either 30-year annual or seasonal averages. When added in the β_0 position, the effects are additive to the position, tree and plot level variables.

Monthly climatic variables were geographically interpolated for each plot for the 30 years prior to felling of the sample tree with the Biosim software ([Régnière et al., 1995](#); [Régnière and Saint-Amant, 2008](#)). Mean 30-year seasonal (winter: December, January, February; spring: March, April, May; summer: June, July, August; fall: September, October, November, December) precipitation sum (mm) and temperatures (°C) were then computed. Annual mean temperatures, rainfall (in mm) and snowfall (in water equivalent, mm) over the last 30 years were also computed.

All statistical analyses were performed using the R statistical software ([R Development Core Team, 2008](#)). Prior to inclusion in the fixed part, a preselection of the most important seasonal variables was carried out with a linear regression using the site random effect estimates (e.g. $b_{i,1}$ and $b_{i,2}$). The site random effects were obtained from the model without any climatic variables (i.e. from Eq. (1) as presented in [Schneider et al., 2013](#)). Collinear variables were eliminated using the variance inflation factor with a threshold of 5% ([Quinn and Keough, 2002](#)) using the ‘vif’ function from the car package in R ([Fox et al., 2014](#)). The climatic variables were then selected using Akaike’s Information Criterion (AIC) model selection approach ([Burnham and Anderson, 2002](#)) using the ‘aictab’ function from the AICcmodavg package in R ([Mazerolle, 2015](#)). The best model was the model with the lowest AIC. The selected seasonal variables were then inserted into

Eq. (1) as:

$$\alpha = \alpha' C_{\alpha} \quad (3)$$

and into Eq. (2) as:

$$\beta_0 = \beta' C_{\beta} \quad (4)$$

where C_{α} and C_{β} are the matrices of the pre-selected seasonal variables (of dimensions: number of observations (number of rows) X number of parameters (number of columns, +1 for C_{α} in order to have an intercept)) and α' and β' vectors of estimated fixed effect parameters. In the case of the annual climatic variables, C_{α} and C_{β} are composed of the 30-year mean temperature, rainfall and snowfall, i.e. with no preselection. Eq. (1) was fitted with the nlme package in R (Pinheiro et al., 2010).

2.5. Estimating tree volume and its change with global change scenarios

Tree volume was estimated from the taper equation by numerically integrating the volume of 0.10 m section from stump height (0.15 m) to tree apex, as no closed form analytical solution is possible (Fortin et al., 2013). The diameters of each section end were predicted using Eq. (1), and the volume obtained using Smalian's formula (Loetsch et al., 1973), which considers a log being a second-degree paraboloid (Eq. (5)).

$$v_{ij} = \sum_{k=1}^{q-1} \frac{\pi \times 0.10}{1000^2} \left(\frac{\hat{d}_{ijk}^2 + \hat{d}_{ijk-1}^2}{4} \right) \quad (5)$$

where q is the number of sections ($q = [HT_{ij} \times 10] + 1$, and $h_{ijq} = HT_{ij}$).

The effect of the different climatic variables was then explored by (i) comparing separately the changes in stem volume using 10th and 90th percentile of each climatic variable entered into the model and (ii) by comparing individual tree volume using the projected global change scenarios with the least and most important changes (IPCC, 2013).

Climatic scenarios for north-eastern America from 2000 to 2100 were extracted from the IPCC fifth assessment report (IPCC, 2013, p. 1279). Among the scenarios exposed in the report, the scenarios leading to a moderate and a severe change were retained. These scenarios predicted the variation of annual, winter and summer temperature and precipitation. Autumn and spring variation in climatic variables were obtained by averaging summer and winter variations. It was assumed that the variations in snowfall would vary in the same way as those presented for precipitation sums. All climatic scenarios are described in Table 2.

These changes were then related to three functional traits: water-logging tolerance (ranging from 0 (very intolerant) to 6 (very tolerant), Niinemets and Valladares, 2006), drought tolerance (ranging from 0 (very intolerant) to 6 (very tolerant), Niinemets and Valladares, 2006) and shade tolerance (ranging from 1 (very tolerant) to 9 (very intolerant), Humbert et al., 2007). Each species had one value for each trait. Finally, the effects of shifts in stem form on biomass estimation were then estimated using biomass allometric relationships proposed by Lambert et al. (2005), by assuming that the change in stem biomass was directly proportional the change in total stem volume.

Table 2
Changes in annual and seasonal climatic variables under moderate and severe global changes.

		Annual	Winter	Spring	Summer	Autumn
Temperature	Moderate	+1 °C	+0.7 °C	+0.85 °C	+1 °C	+0.85 °C
	Severe	+4.2 °C	+4.8 °C	+4.8 °C	+4.8 °C	+4.8 °C
Precipitation	Moderate	−2%	−4%	−5.5%	−7%	−5.5%
	Severe	+14%	+20%	+17%	+14%	+17%
Snowfall	Moderate	−2%	−	−	−	−
	Severe	+14%	−	−	−	−

3. Results

Models were fitted by inserting the climatic variables alternately in the α (Eq. (3)) and β_0 terms (Eq. (4)) and simultaneously in the two terms. For both the seasonal and annual models, the addition of the climatic variables in α and β_0 terms lead to the lowest AIC (Table 3), when compared to the models with the climatic variables in only one term and the models without climatic variables. The model with seasonal variables had the lowest AIC for white birch, black spruce and balsam fir whereas the model with annual variables showed the best fit statistics for trembling aspen and white spruce.

For the models with 30-year average annual climatic variables, α was found to be proportional to snowfall for trembling aspen and black spruce, and inversely proportional for white spruce and balsam fir (Table 4). Furthermore, β_0 was found to be proportional to snowfall for all the studied tree species. In the case of the models with 30-year average seasonal climatic variables, α was found to be proportional to the summer precipitations for white birch, white and black spruce and balsam fir and β_0 inversely proportional to the summer precipitations for balsam fir and proportional for trembling aspen (Table 5).

The effects of an individual variable, especially if it is found in both the α and β_0 terms are hard to interpret individually, and thus must be determined by either examining the taper curves, or the change in tree volume. The importance of the change in volume is difficult to visualize using taper curves. For example, the taper of an average white birch tree decreased with increasing summer temperatures and winter precipitations (Fig. 2). The differences between the 10th and 90th percentiles tapers were not large in some cases. The volume of the tree, obtained by numerically integrating the stem taper, at the 10th summer temperature percentile was 0.2459 m³, whereas it was 0.2344 m³ for the 90th percentile, leading to a difference of 0.0115 m³, or 4.68% (Table 6).

It thus becomes apparent that at an annual scale, tree volume increases with higher mean annual temperatures (between 0.61% and 3.16%, Table 6), whereas it decreases with larger mean annual rainfall (between 1.04% and 5.87%, Table 6). The effect of snowfall is not equivocal: balsam fir and white birch trees have lower stem volumes when snowfall is higher while the inverse is observed for trembling aspen and black spruce.

When the effects of temperature and precipitation are decomposed by season, the effects vary according to species (Table 6). For example, the overall effect of mean annual temperature on tree volume was positive for all species when temperature was statistically significant. However, for both broadleaved species, higher mean summer temperatures led to trees with smaller stem volumes for same sized trees, whereas higher mean winter temperatures imply trees with larger stem volumes. The inverse was observed for the coniferous species, where trees grown in climates with higher temperatures in the summer and fall had larger stem volumes.

The effect of global change on stem form is thus complex, as several climatic variables are forecast to change and the individual effects of two given climatic variables can be opposite for two species. Changes in individual tree volume are more important for taller trees, when trees grown under conditions similar to those of the last 30 years and those under both moderate and severe climatic scenarios are compared (Fig. 3). Illustrated in Fig. 3 is the relative change in volume, between the volume predicted by the taper of a tree under current conditions and a tree under one of the two retained global change scenarios.

As can be seen in Fig. 3, the interaction between the climate and diameter at breast height is not important. In fact, the relative change in volume does not vary with DBH. The inverse is however observed for height, where the relative difference between actual and predicted volumes under the global scenarios increases as trees are taller (Fig. 3).

For both trembling aspen and black spruce, the most important changes were observed for the scenario with the most severe changes (trembling aspen: 1.3% for severe changes vs 0.3% for moderate

Table 3

Akaike's Information Criterion (AIC) for the model without climatic variables (Original), with 30-year annual averages (Annual) and 30-year seasonal (Seasonal) climatic variables. Bold faced AICs indicate the lowest value for a given species. n.c indicates that the model was not able to converge.

Model	Position of climatic variable	Trembling aspen	White birch	White spruce	Black spruce	Balsam fir
Original		222 300.3	138 998.2	324 143.2	549 273.3	619 169.3
Annual	α term	222 297.4	138 984.5	324 122.7	549 053.5	618 962.8
	β_0 term	222 298.3	138 990.1	324 136.9	549 243.6	619 161.7
	Both α and β_0	222 244.1	138 977.1	324 115.3	549 028.0	618 955.1
Seasonal	α term	222 250.7	138 978.6	324 118.1	549 007.4	618 964.3
	β_0 term	222 298.7	138 986.6	n.c.	549 201.0	619 152.3
	Both α and β_0	222 249.2	138 966.8	n.c.	549 000.8	618 947.7

Table 4

Parameter estimates (standard errors in parentheses) for the model with 30-year mean annual climatic variables.

Position of the climatic variable	Climatic variable	Trembling aspen	White birch	White spruce	Black spruce	Balsam fir
α (Eq. (9))	Temperature	0.0271 (0.0098)	−0.0349 (0.0134)		0.0579 (0.0059)	0.0221 (0.0062)
	Rain		0.0011 (3e−04)	5e−04 (1e−04)	6e−04 (2e−04)	0.0011 (1e−04)
	Snow	0.0013 (2e−04)		−5e−04 (1e−04)	2e−04 (9.3e−05)	−3e−04 (9.8e−05)
β_0 (Eq. (10))	Temperature				0.0028 (0.0012)	0.0101 (0.0022)
	Rain				−2e−04 (3.2e−05)	−1e−04 (4.4e−05)
	Snow	2e−04 (7.6e−05)	4e−04 (9e−05)	1e−04 (3.9e−05)	1e−04 (3.3e−05)	1e−04 (4.3e−05)

Table 5

Parameter estimates (standard errors in parentheses) for the model with 30-year mean seasonal climatic variables.

Position of the climatic variable	Climatic variable	Season	Trembling aspen	White birch	White spruce ^a	Black spruce	Balsam fir
α (Eq. (9))	Temperature	Summer	−0.0935 (0.0168)	−0.061 (0.0181)			
		Fall			0.0375 (0.0079)	0.0762 (0.0059)	
		Winter	0.0517 (0.0068)	0.0243 (0.0075)			0.0418 (0.0031)
	Precipitation	Spring				0.0022 (3e−04)	
		Summer		0.0015 (5e−04)	0.002 (5e−04)	0.0028 (4e−04)	0.0027 (3e−04)
		Fall			−0.0016 (6e−04)	−0.0025 (5e−04)	
		Winter					−0.0013 (2e−04)
β_0 (Eq. (10))	Temperature	Summer		0.0236 (0.0091)		−0.0043 (0.0014)	−0.0071 (0.003)
		Winter		−0.0137 (0.0043)			0.006 (0.0012)
	Precipitation	Summer	3e−04 (1e−04)				−2e−04 (1e−04)
		Winter		0.001 (2e−04)			

^a Climatic variables only in alpha position, as the other models did not converge.

changes; black spruce: 2% vs 0.8%; Fig. 3). For balsam fir, the inverse was observed (4.5% vs −1.2%, Fig. 3). This is also the case for white spruce, the changes were however so small that they can be considered biologically non-significant (differences in volume between actual and projected climates < 0.5%, Fig. 3). Finally, shifts in stem volume due to changes in climate were approximately the same under both scenarios for white birch (−4.5% vs −4%, Fig. 3).

The largest shifts in stem volume induced a 3–4% change in total tree biomass (Table 7, Appendix 4). This thus implies that if wood density does not change, the biomass of an individual trembling aspen tree would increase by 0.93% under the severe climate change scenario and 0.2% under the moderate change, whereas black spruce would increase by 1.4% and 0.56%, respectively, under both scenarios. A balsam fir tree would increase its biomass by 4.5% under severe

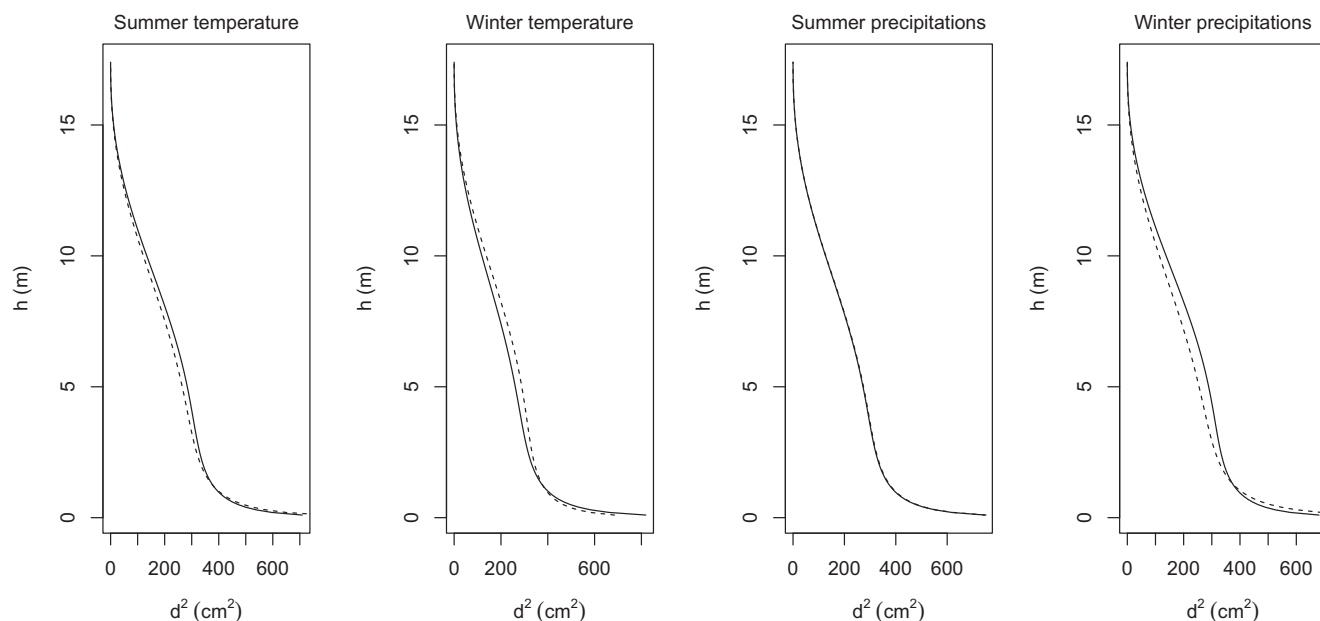


Fig. 2. Differences in stem taper (diameter squared d^2 at given height h) between the 10th (solid line) and 90th (dotted line) percentiles of summer and winter 30-year mean temperatures and precipitations as predicted with the model parameter estimates (Table 4) for an average white birch tree (diameter at breast height (DBH) = 197 mm, total tree height (HT) = 17.4 m). All other variables set at their average values, for changes in illustrated variable.

changes, or decrease by 1.2% under the moderate change scenario. Finally, the change of -4.5% and -4% in volume observed for white birch would translate to a decrease in biomass of 3% and 2.66%, respectively.

Inter-species changes in stem volume with temperature were negatively related to the shade tolerance index whereas inter-species changes in stem volume with rainfall were positively related to waterlogging tolerance index (Fig. 4). No relationship between drought tolerance and inter-specific changes in stem volume with any climatic variable was found. The same trends were observed for changes in stem volume following both the moderate and severe global change scenarios (Fig. 5), with little differences in the change in volume to trait relationship between both scenarios.

4. Discussion

In order to evaluate the biomass of a forest, both the volume and basic density of the different compartments of the trees (e.g. branches, foliage, stem and roots) are needed. Often, the simulation of biomass trajectories with global change takes into account tree diameter and

height variations and consider that basic density as constant (Solberg et al., 2009; Bellassen et al., 2010) even if variations in wood density have been demonstrated to be of importance on biomass computations (Baraloto et al., 2011). In addition, it has long been known that basic density is under a strong influence of climate. For example, ring basic density of coniferous species has been positively related to an increase in summer temperatures, whereas forests with more precipitations have trees with lower ring basic density (D'Arrigo et al., 1992; Wang et al., 2002; Savva et al., 2010; Franceschini et al., 2013). Based on these results, trees undergoing the moderate global change scenario would have a lower basic density as the increase in precipitations is of larger magnitude than the increase in temperature. The severe global change scenario is expected to result in basic density increase as the temperatures would rise and precipitations fall. Estimates in biomass changes would thus follow these results, if no changes in stem volume occur, for forests with the same characteristics (e.g. density, size and species composition).

However, the results presented here indicate that tree form is not only related to forest characteristics (e.g. Appendices 1, 2 and 3), but also to the climate under which the trees grow. For white birch, both

Table 6

Comparison of the 10th and 90th percentile changes in individual tree volume (with the all other variables set at the average value for the species), with negative values indicating that the volume of a tree of the 10th percentile is greater than that of the 90th percentile. Absolute values in m^3 , relative values in percentage in parentheses. Bold characters indicate values for the best model for each species (see Table 1).

Model	Variable	Season	Trembling aspen	White birch	White spruce	Black spruce	Balsam fir
Annual	Temperature			0.0037 (1.66)	0.0032 (0.61)	0.0059 (2.9)	0.0078 (3.16)
	Rain		-0.0068 (-1.04)	-0.0135 (-5.87)	-0.0152 (-2.85)	-0.003 (-1.47)	-0.0049 (-1.95)
	Snowfall		0.0062 (0.95)	-0.0024 (-1.08)		0.0014 (0.66)	-0.0049 (-1.91)
Seasonal	Temperature	Summer	-0.0108 (-2.13)	-0.0115 (-4.68)		0.0017 (0.76)	0.0047 (1.46)
		Fall			0.0011 (0.19)	5e-04 (0.23)	
		Winter	0.0155 (3.16)	0.017 (7.31)			-0.0093 (-2.85)
	Precipitation	Spring				4e-04 (0.18)	
		Summer	-0.0189 (-3.64)	0.0016 (0.67)	0.0027 (0.49)	9e-04 (0.43)	0.0104 (3.33)
		Fall			-0.001 (-0.18)	-4e-04 (-0.16)	
		Winter		-0.0202 (-8.13)			-6e-04 (-0.19)

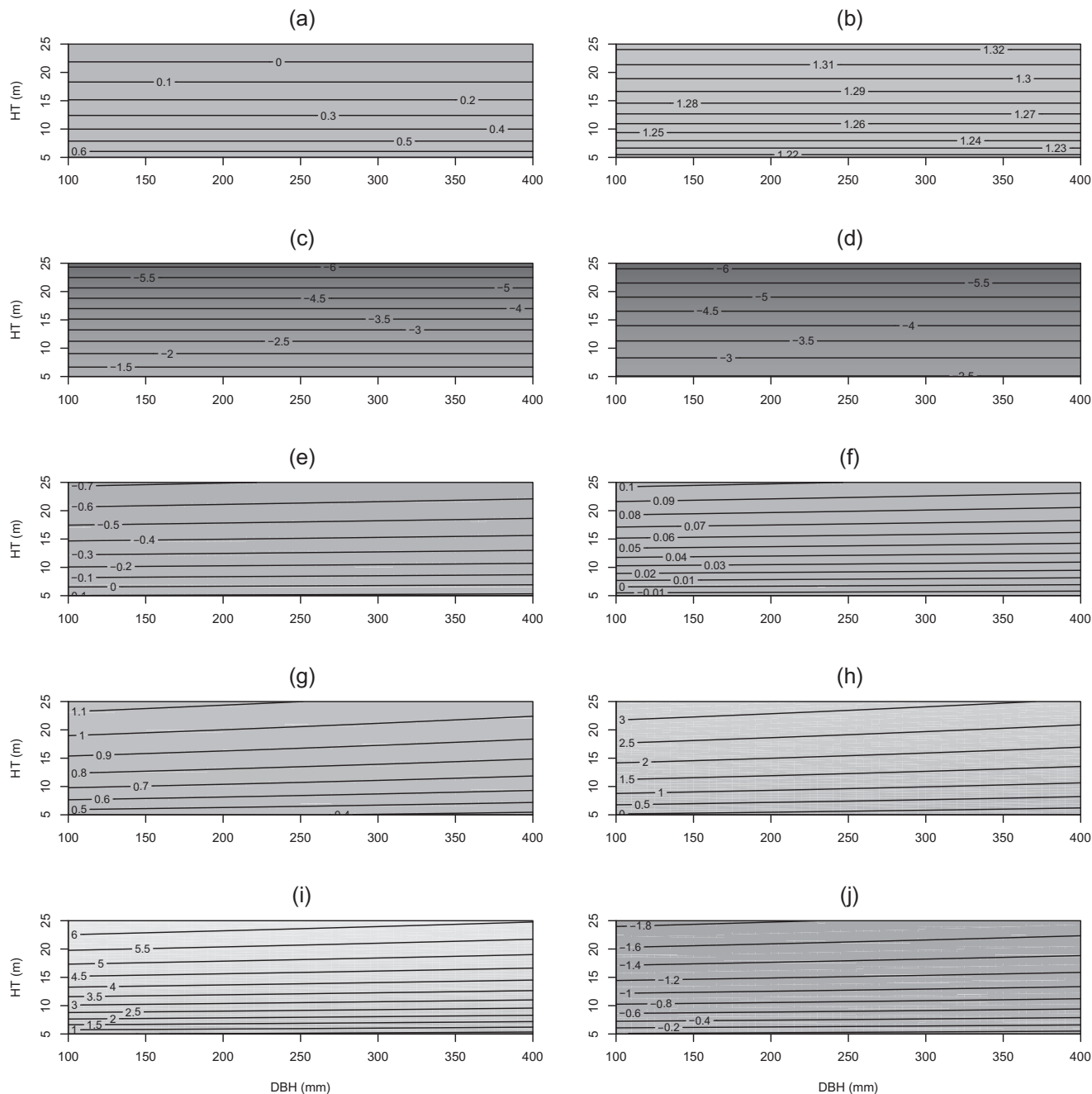


Fig. 3. Relative differences (%) in individual tree volume with diameter at breast height (DBH) and total tree height (HT) as predicted by the model with the lowest AIC per species, when comparing 2 climatic change scenarios (least change: plots a, c, e, g and i; most change: b, d, f, h and j) with the mean climate variables for the past 30 years for trembling aspen (a, b), white birch (c, d), white spruce (e, f), black spruce (g, h) and balsam fir (i, j).

Table 7
Change in biomass per species (in %) with change in tree volume (in %) for a 20 cm DBH tree based on the allometric relationships from Lambert et al. (2005).

Percent change in volume	Trembling aspen	White birch	White spruce	Black spruce	Balsam fir
–5.0	–3.56	–3.33	–3.38	–3.5	–3.21
–2.5	–1.78	–1.66	–1.69	–1.75	–1.61
2.5	1.78	1.66	1.69	1.75	1.61
5.0	3.56	3.33	3.38	3.5	3.21

moderate and severe climatic change scenarios would lead to trees with more taper and with therefore a volume 5% lower for a tree of same dimensions, all other things being equal. In contrast, the same climatic

scenarios would lead to less tapered black spruce and thus with a volume 1–2% higher. These comparisons hold for trees with the same dimensions (dbh and total height) found in stands with the same basal area and density. Global change will also influence stand dynamics, which in turn will modify both stand basal area and stand density. There will most probably be a compounding effect of global change on stem form.

The links between climate and tree growth have seen a lot of research. For example, an increase in growing season temperature was found to decrease black spruce diameter growth as a consequence of higher summer evapotranspiration (Subedi and Sharma, 2013). In addition, although higher temperatures increase photosynthesis, the increase in respiration is more important, leading to a decrease in carbon available for growth (Way and Sage, 2008; Girardin et al., 2016). White

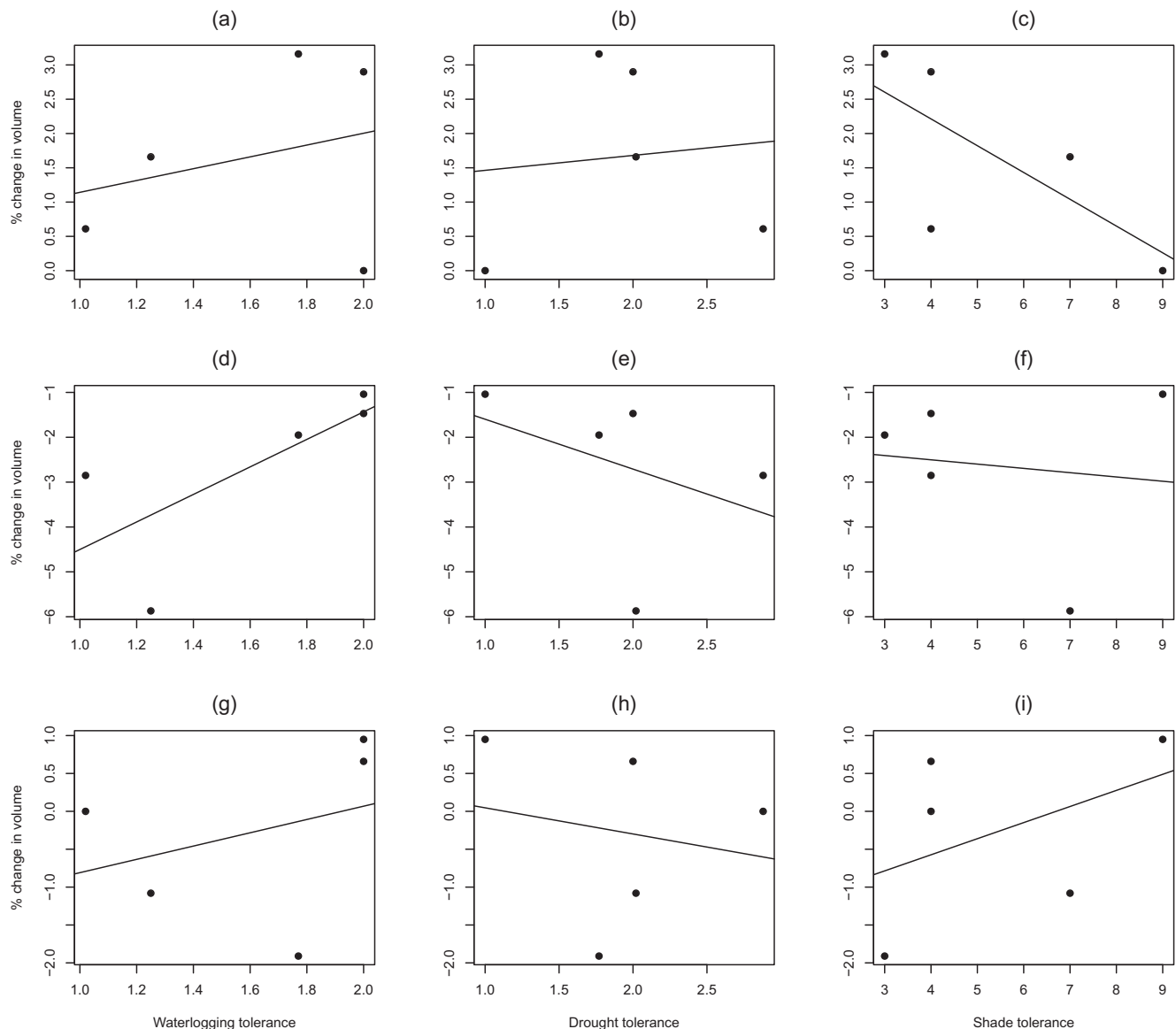


Fig. 4. Relative differences (%) in individual tree volume between 10th and 90th annual percentiles (temperature: a, b, c; rainfall: d, e, f; snowfall: g, h, i) in individual tree volume versus waterlogging (a, d, g), drought (b, e, h) and shade (c, f, i) tolerance for average tree sizes for each species.

birch and trembling aspen growth was however more correlated to the amount of precipitations (Huang et al., 2010).

Most of the climate-growth studies consider only radial growth at a given height, and do not take into account the changes in the growth distribution along the stem. Indeed, the sensitivity of the relationship between ring width and climate varies with height within the tree for a large number of species (Kerhoulas and Kane, 2012; van der Maaten-Theunissen and Bouriaud, 2012). Rings formed closer to the stem apex show a stronger correlation with climatic variables than rings at the base of the tree, and is explained by path length hydraulic limitations. As stem taper is the sum of the rings at a given height, it is normal to observe shifts in stem form with climatic variables, such as those observed in this study.

Stem form was found to change with climatic variables, and the direction of the change (decrease in volume due to more taper versus increase in volume due to less taper) was found to be linked to two functional traits: waterlogging and shade tolerance. Waterlogging tolerance classifies species according to their ability to withstand a reduction in root-zone soil oxygen availability (Niinemets and Valladares,

2006) whereas shade tolerance ranks species based on their capacity to grow under low light (Humbert et al., 2007). Our results indicate that species with higher waterlogging and shade tolerance tend to decrease their stem taper (and thus increase stem volume for a same DBH and total height) with an increase in temperature. These species are thus less prone to hydraulic limitations, as their rings close to the apex should be larger than those at the base of the tree. The shifts in stem taper could thus explain the recently reported changes in primary to secondary growth allocations (Franceschini et al., 2016).

As stem biomass can account for 65–70% of the biomass of a tree (Lambert et al., 2005), small changes in stem volume can change biomass estimates. Based on the biomass allometric equations provided by Lambert et al. (2005), an increase in 5% in tree volume will thus translate to a change a 3–4% increase in biomass of a single tree, which would be the equivalent to an increase in 3–4 kg of biomass per tree. Thus scaling from a tree to a stand or a forest that generally have between 900 and 1600 trees per hectare, the differences when taking into account the changes in stem form with climate have implications on the estimation of future carbon stocks contained within a forest.

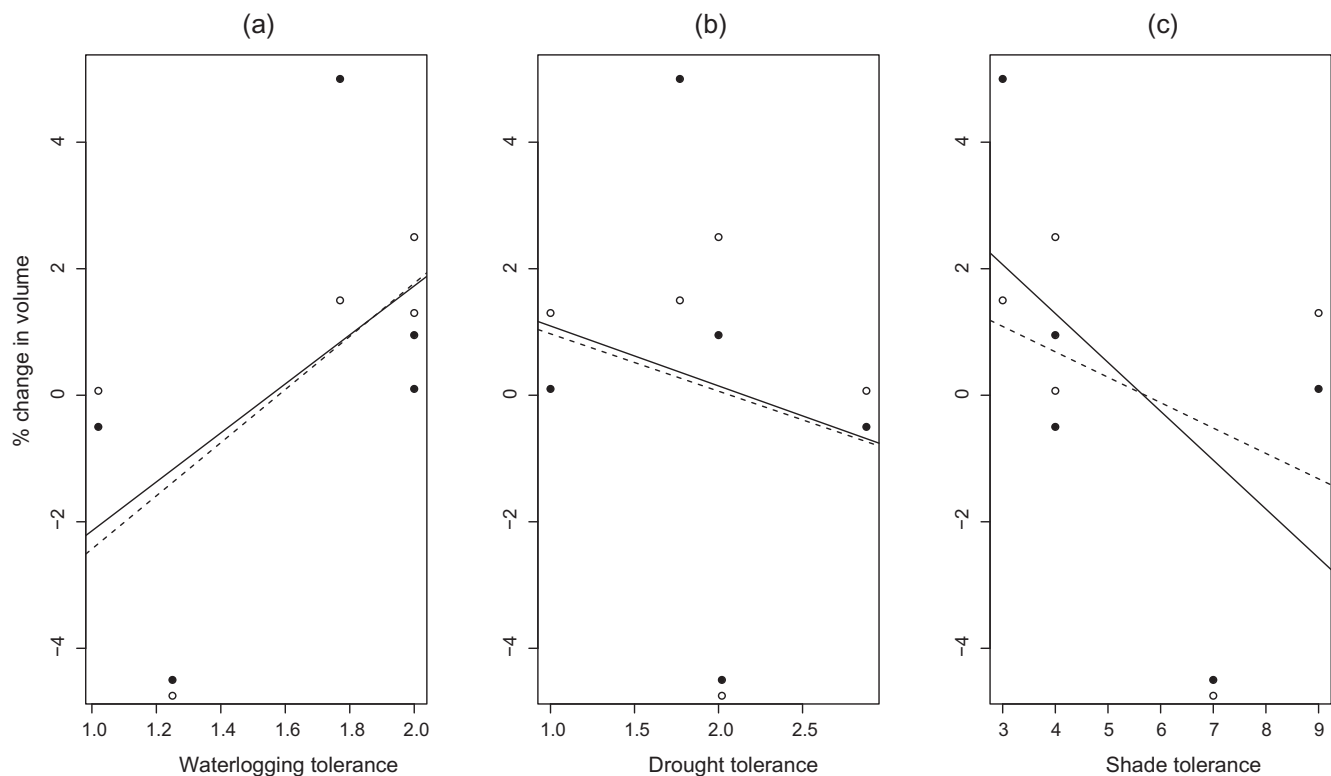


Fig. 5. Relative differences (%) in individual tree volume between actual and future forecasted climatic values (moderate changes: full dots and line; severe changes: empty dots and dotted line) versus waterlogging (a), drought (b) and shade (c) tolerance for average tree sizes for each species.

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Data accessibility

The data is the property of the Ministry of Forests, Wildlife and Parks of the Government of Quebec (Ministère des forêts, de la faune et des parcs). It can be accessed by contacting the Inventory Branch (<http://www.mffp.gouv.qc.ca/forets/inventaire/produits-donnees-inventaire.jsp>).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.12.026>.

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